

## Final Report

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Much has been written about the need to move from chamber studies to FACE-type experiments. Some of the reasons initially postulated have been supported (*e.g.*, whole ecosystems with real nutrient cycles) and others have not (*e.g.*, photosynthetic responses are similar in greenhouse and OTC/FACE studies). In the area of ecosystem science, particularly in forest ecosystems, FACE technology has proven invaluable in understanding ecosystem-level carbon sequestration, with results often being novel and contradictory from those in controlled environments. The following are findings reported by the end of 2006, followed by more recent citations, the latest of which focused on a model-data synthesis activity involving both Duke and ORNL FACE sites.

### 1. The major findings of the elevated carbon dioxide at Duke

#### General findings:

- **North American forests will absorb and retain more carbon as atmospheric [CO<sub>2</sub>] increases; the increase in the rate of carbon sequestration will be highest on nutrient-rich soils with no water limitation, and decrease with decreasing fertility and water supply.**
- **North American forests will not reduce the amount of water they use as atmospheric [CO<sub>2</sub>] increase, and in the long-term will require large quantities of soil N to support high rates of carbon sequestration with rising atmospheric [CO<sub>2</sub>].**

#### Major findings on specific processes leading to these generalities:

- **Photosynthesis** will increase, but less than expected based on physiological studies because of negative feedbacks at the leaf level (biochemistry) and canopy level (reduced light and conductance with increasing leaf area index, LAI). (1; 2).
- **Plant respiration** will increase in proportion to the increases in tree growth and amount of living biomass only—elevated [CO<sub>2</sub>] will not affect tissue specific respiration.
- **Net primary production (NPP)** will increase where nutrients are not limiting. Under severe nutrient limitation—NPP will not increase at all (3). In moderately fertile and fertile soils, NPP will increase ~23% (median of four “forest” FACE experiments; 4), similar to early reports from controlled environment studies (5, adjusted for differences in experimental conditions) but much less than the average reported in other reviews (6; 7). At low LAI the enhancement will be largely driven by an enhancement in LAI whereas at high LAI, the enhancement will be largely driven by increased light-use efficiency (4; 8). The sustainability of the NPP response will depend on soil fertility (7; 3, 9).
- **NPP** in intermediate fertility sites may undergo several phases of transient response, but it is clear that initial responses will include a pulse of productivity. In low to moderate fertility sites, the initial pulse in productivity is likely to be followed by an attenuation of the NPP response as a result of *progressive nitrogen* (or more generally *nutrient*) *limitation*, PNL (10; 11; 12; 13; 9; 14). In high productivity sites the initial response will likely be sustained.
- **Carbon partitioning to pools with different turnover times** is controlled by soil resources. With increasing soil nutrient supply, stands under elevated [CO<sub>2</sub>] diverge in LAI from stands under ambient [CO<sub>2</sub>] with impacts on the following:
  - **Aboveground NPP** (ANPP’, including construction and maintenance respiration) increases with LAI (8), without additional effects of elevated [CO<sub>2</sub>].
  - **The fraction of ANPP’ allocated to wood**, a relatively slow turnover pool, *increases* with LAI in *broadleaf* FACE experiments (~50% at low LAI, reaching a maximum of 70% at moderate LAI), with the effect of elevated [CO<sub>2</sub>] on allocation entirely accounted for by changes in LAI.

In *pinus*, allocation to wood *decreases* with increasing LAI (from ~65% to 55%), but was higher (~68% to 58%) under elevated [CO<sub>2</sub>] at any level of LAI (8).

- o **Total carbon allocation belowground and CO<sub>2</sub> efflux from the forest floor** decrease with increasing LAI, but the enhancement under elevated [CO<sub>2</sub>] is constant (~22%) over the entire range of LAI (15; 16)
- o About a third of the *extra* carbon allocated belowground under elevated [CO<sub>2</sub>] is retained in **litter and soil storage** at the US FACE sites (16). At Duke FACE, a third of the incremental carbon sequestration is found in the forest floor, but there is little or no net incremental storage of carbon in the mineral soil (17), despite evidence of greater turnover at those depths.
- **Nitrogen cycling and availability controls LAI and thus NPP:**
  - o Fertilizing in nutrient-limited sites shifts carbon allocation aboveground and depresses the cycling of extra photosynthate fixed under elevated [CO<sub>2</sub>] back to the atmosphere (18; 16).
  - o The availability of soil nitrogen (N) controls the productivity response of forests to rising concentrations of atmospheric CO<sub>2</sub> (7). The range of responses encompasses no response to elevated [CO<sub>2</sub>] in the most N limited forests (3), to >100% stimulation of NPP in productive soils (19). A shift in allocation from wood to fine roots with elevated [CO<sub>2</sub>] in broadleaf species is consistent with increasing nutrient limitation through time (20).
  - o Rapid forest growth under elevated [CO<sub>2</sub>] increases N uptake from soil depleting soils of labile pools of N (21; 14). The immobilization of N in biomass, not litter feedbacks or microbial-N immobilization, is the most likely cause of progressive N limitation (10).
- **Heterotrophic respiration** increases due to increasing quantities of readily decomposable materials from leaf litter-fall, fine-root and mycorrhizal hyphae, and root exudate (2).
- **Soil acidification and rock weathering** increases under elevated [CO<sub>2</sub>], but yields only a small potential for carbon sequestration over a geological time scale (22)
- **Water use** is not lower under elevated [CO<sub>2</sub>]. At the Duke FACE site, stomata of pines do not respond directly to elevated CO<sub>2</sub>. Rather, the CO<sub>2</sub>-induced increase in LAI causes a reduction in stomatal conductance due to self-shading lower in the canopy (23). In sweetgum (ORNL FACE) stomatal closure under elevated [CO<sub>2</sub>] is modest and combined with limited canopy-atmosphere coupling, results in little effect on water-use at the canopy scale (24).
- ❖ **There is little doubt that canopy photosynthesis will increase with rising concentrations of atmospheric CO<sub>2</sub>. In moderate to high fertility sites, aboveground biomass production will be the dominant sink for the extra photosynthate fixed under elevated CO<sub>2</sub>. In low to moderate fertility sites, the extra photosynthate fixed under elevated CO<sub>2</sub> will be allocated belowground, where heterotrophic organisms will rapidly cycle carbon back to the atmosphere as CO<sub>2</sub>.**

## 2. Common and distinct insights learned about the sustainability of future terrestrial ecosystem carbon sinks from FACE and OTC studies

To assess “*the sustainability of future terrestrial ecosystem carbon sinks*” with a rising concentration of atmospheric CO<sub>2</sub>, it is critical to understand how elevated [CO<sub>2</sub>] affects the rate at which other, limiting soil resources are supplied. Although elevated [CO<sub>2</sub>] is unlikely to affect water use, the effect of elevated [CO<sub>2</sub>] on soil N supply is still uncertain, and a major area of research.

The time scale (~10 years or less) over which FACE/OTC experiments are currently conducted is too short to assess sustainability. However, the following findings are emerging:

- Elevated [CO<sub>2</sub>] indicates the presence of an enhanced sink for atmospheric CO<sub>2</sub> by increasing terrestrial productivity ~23±2% above that under ambient [CO<sub>2</sub>] (4).
- The largest enhanced sink for atmospheric CO<sub>2</sub> is biomass (25). The increased accumulation of C in soil, although present, is generally small by comparison (26).

- The availability of soil N and water constrains the productivity response of forests to high concentrations of atmospheric CO<sub>2</sub> (19; 3)
- In biomass, wood represents the largest, long-term sink for atmospheric CO<sub>2</sub>. The strength of the woody biomass sink is dictated by the availability of soil N (3). As soil-N availability increases, carbon allocation belowground decreases and woody biomass production increases (16).
- Based on the Duke FACE, forest ecosystems suffer less physical and insect damage to the canopy and recover more rapidly under elevated [CO<sub>2</sub>] (27; 28; 29) thereby maintaining a stronger sink strength through time.
- ❖ In forest ecosystems, leaf-area index (LAI) is an excellent predictor of NPP and the allocation of NPP to pools of different turnover times under current and future [CO<sub>2</sub>].

### 3. Unanswered major questions about the functioning of ecosystems

- The sustainability of terrestrial carbon sinks is poorly understood. Nearly all ecosystem experiments have lasted from several months to several years. Feedbacks to nutrient cycles take years to decades to develop, and with nutrient limitation as a fundamental constraint to terrestrial productivity (30), insufficient time has elapsed to determine whether sinks for rising concentrations of atmospheric CO<sub>2</sub> are sustainable through time.
- It is unknown whether changes in the N cycle follow or control changes in the carbon cycle under elevated CO<sub>2</sub>. The theory of progressive N limitation argues for the control of ecosystem responses to elevated [CO<sub>2</sub>] by the availability of N, a hypothesis supported to varying degrees in different ecosystems. By contrast, the uptake of N from soil dominates over N-use efficiency as the mechanism supporting short-term, high rates of NPP under elevated [CO<sub>2</sub>] in forested ecosystems (31). The belowground processes responsible for greater rates of N uptake are still poorly understood making it difficult to predict the sustainability of responses through time (32).
- It is unknown whether elevated [CO<sub>2</sub>] simply accelerates the rate of forest stand development or whether elevated [CO<sub>2</sub>] increases the C storage capacity of forests beyond that under ambient concentrations of atmospheric CO<sub>2</sub>.
- It is unknown how inter-annual variations in climate affect forest productivity directly and indirectly through changes in nutrient cycling. Time-series data are required to disentangle the interactive effects of climate, soil N availability and atmospheric [CO<sub>2</sub>] on terrestrial C storage, and the current generation of FACE/OTC experiments is only beginning to generate records of sufficient length to address these questions.
- ❖ Added manipulations (e.g., Ozone at Aspen FACE, N at Duke FACE) permit to push the system by disturbing the autotrophic source-sink relationship, thereby impacting the route and rate of carbon transfer to the heterotrophic system. Differences between the source and the integrated fluxes are responsible for carbon sequestration in pools of different longevity. **Quantitative expression of the processes controlling these fluxes, essential for modeling and scaling carbon sequestration to regions and beyond, must rely on long time series.**

### 4. The impact of FACE/OTC studies on our understanding of future carbon cycles at the regional and global scales

- Forest FACE experiments show that the short-term, median response of NPP to rising concentrations of atmospheric CO<sub>2</sub> is 23±2%, an average response that is conserved among forests widely differing in productivity (4). However, the variability in the response even within these homogeneous sites can be large (<10% to >100%); at Duke FACE this was shown to reflect local variation in available N. The absolute magnitude of the additional sink strength is highly variable

among years; at Duke FACE much of this variability is caused by stand development and droughts (8).

- Forest FACE experiments show that the uptake of N from soil is the primary, short-term mechanism supporting high rates of atmospheric CO<sub>2</sub> sequestration (31). The dependence on an external supply of N rather than an increase in N-use efficiency implies that regional and global scale sequestration cannot be sustained in the absence of increases in an exogenous supply of N.
- Recognizing that both CO<sub>2</sub> and N control terrestrial productivity, FACE/OTC studies show that the terrestrial sink predicted by the third IPCC assessment is too large (33). Most global-scale models are driven by climate, light-use efficiency and atmospheric concentrations of CO<sub>2</sub>, with the photosynthesis-CO<sub>2</sub> relationship established from a long-history of elevated CO<sub>2</sub> research (34). The recent generation of FACE/OTC studies show that global models that are not constrained by spatial and temporal variability in N availability, N uptake, the photosynthesis-N relationship and the stoichiometry of C:N in biomass production will over predict terrestrial C sequestration with rising concentrations of atmospheric CO<sub>2</sub>.
- The Duke FACE and ORNL FACE sites are dominated by *Pinus taeda* and *Liquidambar styraciflua*, respectively, species that are widespread throughout the southeastern US super region. Given stand age, the longevity of these experiments and explicit manipulations of soil N availability, these sites have contributed to a regional understanding of C sinks and future timber production. The studies also dispel recent assertions (35) that increases in stream flow in the U.S. are likely the results of decreases in stomatal conductance with increase in atmospheric [CO<sub>2</sub>]. Thus water shortages will not become more infrequent in the future except where climate change is associated with a marked increase in precipitation (36; 37)
- ❖ The observation that changes in LAI are good predictors of NPP and its allocation under elevated [CO<sub>2</sub>] has already attracted attention of modelers intending to use such information to test their models, or as a convenient allocation rule in biogeochemical models that rely on remotely sensed LAI as input.

## 5. Additional accomplishments from the research

- Several ancillary studies at the Duke FACE experiment have indicated responses with significant consequences for **human health**.
  - The canopy trees have shown dramatic increases in the production of female (seed) and male (pollen) cones (38, 39). Observations of the latter indicate substantially higher airborne consequences of pollen in future environments, with impacts on asthma, emphysema and hay fever in humans.
  - One of the dominant understory plants in the Duke Forest experiment is poison ivy, which has shown a sustained and substantial (70%) increase in biomass and leaf-specific content of its allergenic compound (usuriol), which potential impacts on human welfare (40).
- **Economic impacts** of timber production (41; 42, 43; 44; 45; 46; 47) has been analyzed and is now updated to account for increasing detail that facilitate better regional scaling:
  - On sites of moderate to high fertility, loblolly pine responds with increased stem growth rate. On very poor sites, both loblolly pine (a shade intolerant species in the humid-warm temperate region) and Norway spruce (a shade tolerant species near the Arctic Circle) respond vigorously to CO<sub>2</sub> if N is also supplied. It is becoming more common for the industry to fertilize poor sites, with the gain certain to increase with atmospheric [CO<sub>2</sub>]. This will lead to shorter rotations.
  - FACE experiments show that where nutrients are not limiting timber production will increase with atmospheric [CO<sub>2</sub>], with potential impacts on regional economies. However, because elevated atmospheric [CO<sub>2</sub>] is a global phenomenon, the economic impact of rising timber

production will require macro-economic analysis, and data from the current generation of FACE experiments are likely to be used in such analyses.

- The potential for **gene flow from genetically engineered transgenic trees** is likely to increase under elevated [CO<sub>2</sub>], with implication to regulatory policy (48).
- Groups **modeling at scales ranging from stands to the continent** have been using data readily available at the Duke FACE archive, investigating processes ranging from progressive N limitation at the stand level to carbon sequestration at the continent (21 groups since the start of the project, with 13 current user groups).

#### **Citations in support pf 1-5 (of >200 published through 2006)**

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## Research since 2007

As the following selected list of citation demonstrate, the final four years of enrichment were dedicated to increasing the length of time series for certain variables (transpiration, net primary production, leaf area index), experiments designed to examine certain processes (stomatal soil CO<sub>2</sub> efflux response to

changing CO<sub>2</sub> concentration, carbon allocation), syntheses of data (photosynthesis), and progressively to modeling. Following the enrichment, two years of monitoring allowed quantifying the effect of step-down in carbohydrate availability on leaf area index, growth, carbon allocation and water use. Progressively since that time, efforts were focused on examination of the skills of a large number of models to correctly estimate the responses of a large number of variables to elevated CO<sub>2</sub> using data from both Duke and ORNL FACE experiments (Medlyn et al., 2015; Zaehle et al. 2014). A partial list of papers published after 2006 is provided below:

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#### Abstract

The Duke FACE experiment increases atmospheric [CO<sub>2</sub>] to a height of 25 m in four 30-m diameter plots, each containing ~100 canopy trees and many sub-canopy individuals. The experiment was initiated in 1994 with CO<sub>2</sub> fumigation of the prototype plot, and reached full CO<sub>2</sub>-fumigation capacity in 1996 when three additional FACE plots came on line. All elevated plots enriched the atmospheric CO<sub>2</sub> concentration by 200 ppmv relative to paired, ambient-CO<sub>2</sub> plots. Formalizing the analysis of CO<sub>2</sub> x N interactions, in March of 2005 each of the six FACE plots established in 1996 was trenched in half, and one half plot fertilized with nitrogen (N) at a rate of 11 g m<sup>-2</sup> yr<sup>-1</sup>, following the approach established in 1998 in the prototype and its reference plot. The δ <sup>13</sup>C of the fumigated plots' atmosphere was -42.6‰, and while the <sup>15</sup>N of the fertilizer did not affect the δ <sup>15</sup>N of tissues directly it greatly reduced the effect of a <sup>15</sup>N tracer study on tissue δ <sup>15</sup>N. The CO<sub>2</sub> enrichment was completed in early November, 2010. Prior to termination of fumigation, 1-8 branches from 4-5 *Pinus taeda* individuals in each half plot were harvested, as well as most *Juniperus occidentalis* and broadleaved individuals <2 cm in diameter (1.4 m aboveground), including vine and herbaceous individuals. Following the termination,

all individuals <8 cm in diameter, followed by all remaining individuals were harvested in half of each plot (a quarter in each CO<sub>2</sub> X N treatment). In all, 189 m<sup>3</sup> of dry material and 826 m<sup>3</sup> of wet material, or a total of 1014 m<sup>3</sup> of material is stored in various suited settings. The project quantified the effect of CO<sub>2</sub> X N on carbon uptake, allocation to various pools, accumulation of carbon in these pools, the release of carbon to the atmosphere, and factors controlling these processes. The project also assessed the effect of CO<sub>2</sub> X N on the components of the water budget, and related processes, as well as on the amount and diversity of understory vegetation.